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SOME EFFECTS OF TEMPERATURE UPON GROWING MICE, AND THE PERSISTENCE OF SUCH EFFECTS IN A SUBSEQUENT GENERATION[1]

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I MUST preface my remarks by an apology for coming before you with some results which have already been published pretty fully within the past year.[2] My appearance here may seem the more unwarranted in view of the limited amount of evidence which I am about to offer upon those subjects which form the focus of attention at this meeting, namely heredity and evolution. However, aside from the fact that I am acting at the instance of our president, I will say two things in my own defense. First, the results which I offer, meager as they doubtless are, appear to be the only ones of just this sort which are in evidence at present.[3] And secondly, I am bold enough to believe that I have developed a promising method of attacking a few of the many knotty problems which are bound up together in the time-honored question: Are acquired characters inherited? It is my hope to convince you that the method which I have employed conforms to certain *a priori* requirements, on the one hand, and, on the other hand, is workable in practise. That my results are not thus far more imposing is due, I think, to no defect in the method itself, but to the limitations which encompass a solitary investigator, deprived of some of the generally acknowledged desiderata for successful work in animal breeding, such, for example, as assistants, funds and adequate equipment.

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[1] Read before the American Society of Naturalists, December 30, 1910.

[2] "Some Effects of External Conditions upon the White Mouse," *Journal of Experimental Zoology,* August, 1909. "The Reappearance in the Offspring of Artificially Produced Parental Modifications," AMERICAN NATURALIST, January, 1910. "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring," *Archiv für Entwicklungsmechanik der Organismen,* June, 1910.

[3] Since writing this statement, I have received Semon's highly interesting paper, entitled 'Der Stand der Frage nach der Vererbung erworbener Eigenschaften" (Fortschritte der naturwissenschaftlichen Forschung, Bd. II, 1910). From this I learn that some of the more important features of my results have been obtained by Przibram, in the course of experiments upon rats, conducted at about the same time as my own. I have not yet seen Przibram's own report of his work. This confirmation will, I trust, dispel any doubts as to the statistical significance of my own figures, whatever interpretation we may choose to give them.

As to the logical requirements for such a test—to begin with, what is it that we are going to test? The "inheritance of acquired characters"?—yes and no. First of all, that threadbare expression itself must be relegated to limbo where it belongs. For, not only does it fail to indicate with any precision the subject-matter of our inquiry, but historically the expression has been applied to a wide range of phenomena, real and alleged. Some of these we now know to be fictitious; others, on the contrary, are acknowledged facts; while others yet are more or less debatable. It is with the debatable group, of course, that we are here concerned. But, even among these, we encounter not one problem but many. Suppose, then, that we drop all vague generalized expressions and consider one more or less restricted problem: *Are specific structural effects, resulting from the action of external conditions upon organisms of one generation ever repeated in the next generation under such circumstances that the immediate and parallel modification of the germ-cells may not be invoked as an explanation?* Under "specific structural effects," I do not wish to include general conditions of health, metabolism, etc.

What are some of the necessary conditions for a fair test of this question? To begin with, we must effect our modifications in the first generation. And since these modifications, if repeated at all, will probably reappear in a much-diminished degree, it would seem far preferable to select characters which lend themselves readily to accurate measurement. Qualitative differences, such as those of color or of physiological reactions, do not seem well adapted to such experiments, although they have commonly been the ones dealt with in studies of this sort.

In the second place, we must choose such an organism and such a physical agency that the latter may act upon the former without immediately influencing the germ-cells. This would seem to rule out of consideration as really crucial tests of this problem all experiments, however instructive otherwise, in which modification has been brought about through the influence of foods, unusual in amount or in character. For the effect of these upon the parent body is, of course, a chemical one, and the specific substances responsible for the modifications are presumably free to enter the germ-cells. The experiments of Arnold Pictet upon lepidoptera and of Houssay upon fowls are to be recalled in this connection. Similar considerations apply with equal force to any results from experiments in which invertebrate animals or "cold-blooded" vertebrates have been influenced by temperature. The recent work of Kammerer upon lizards[4] and that of various investigators upon butterflies and moths occur to us at this point; likewise certain features of Tower's work on *Leptinotarsa.* In such cases, by pretty general consent, we have to do with an "immediate effect upon the germ-plasm," and not with *transmission* at all. Later, I shall inquire a little into the validity of this assumption.

In the meantime, I will point out that for certain classes of animals this objection cannot be raised, at least in its original form. I refer to the so-called "warm-blooded" ones. I am not very well versed in that branch of physiology which deals with temperature regulation, but the published evidence which I have examined seems to show that mammals normally undergo but slight fluctuations of body temperature as a result of even very considerable changes in the temperature of the surrounding atmosphere.[5]

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[4] *Archiv für Entwicklungsmechanik der Organismen,* September, 1910.

Assuming, provisionally, the truth of this proposition, we may discount in advance the objection that the germ-cells of a mammal may be influenced by differences of temperature *as such*. If these differences affect the germ-cells at all, and it is reasonable to believe that they may do so, they must act upon them indirectly.[6] I shall revert to this point again shortly.

As some of you may perhaps already know, I have succeeded for several years past in producing very decided quantitative differences in certain of the external parts of mice through the action of widely differing temperatures. . . . (This part of the discussion has been omitted in the printed report, since the results in question have already been fully published.)

In experiments such as those which I am describing, it is obviously impossible to subject a single individual to both extremes of temperature during growth, and to compare the differing effects of these upon structure. We therefore, of necessity, resort to a comparison of averages, based upon as many individuals as possible. If each of the contrasted groups is sufficiently large, and if its members have been taken at random, the presumption is that the mean potential (that is to say, congenital) value of every character is about the same for the two lots. I fully realize that the study of genetic problems by the use of mass averages has recently received a decided set-back, largely through the labors of some of those who have contributed to our present program. But until some one is ingenious enough to produce a strain of parthenogenetic or self-fertilizing mice, I fear that my only practical method of procedure in these experiments is to deal with mass statistics based upon "heterozygous" stock.

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[5] Przibram found that the body temperature of his rats was somewhat raised when kept in a room at 30° to 35° C. This last was, however, considerably higher than the mean temperature of my own warm room, and the limits of physiological adaptability seem to have been overstepped in his experiments. (See Semon, *op. cit.*, pp. 45, 46.) On the other hand, Pembrey (*Journal of Physiology*, 1895) found that the body temperature of mice did not rise appreciably above the normal when the animals were kept at a temperature of 29.5° or even 32.5° C. for an hour or more. The effects of a more prolonged stay were not determined. I have myself recently commenced experiments with mice, using a special clinical thermometer made for the purpose. I have already (January 21) shown pretty conclusively that mice may have almost precisely the same rectal temperature at — 6° C. as at + 30° C.

[6] The same is true even if humidity, rather than temperature *per se*, is the factor chiefly concerned in these modifications. As stated in my first paper (1909), the relative humidity of my heated room was very much lower than that of the unheated room. Thus far I have not differentiated the effects of these two factors.

It must also be pointed out that the technique of the problem which I am discussing is inevitably different from that involved in the endeavor to find, or to produce, "mutations" or single abrupt deviations from the parent stock, which appear at once in full force, if they appear at all, and thereafter breed true. On the contrary, the distribution of the lengths for the tail, ear and foot, within each of the temperature groups in my experiments, appears to follow the normal probability curve, just as in the case of the so-called "fluctuating variations," whose heritability is nowadays so much in question.

In the splendid paper of Professor Johannsen, to which we listened yesterday, occurs the following statement: "as yet no experiment with genotypically homogeneous cultures has given any evidence for the Lamarckian view, the most extreme 'transmission'-conception ever issued." Leaving aside for the time being the question whether results such as mine, even when every possible defect of technique has been eliminated, are to be regarded as "evidence for the Lamarckian view," let us consider for a moment whether the fact that I have not myself found it practicable to use "genotypically homogeneous cultures" does, in reality, invalidate the evidence which I offer. Apparently Professor Johannsen would hold this to be true. So far as I can see myself, the only difference between results from pure and from mixed lines in the present case would be this. Individuals belonging to a single pure line would probably respond with much greater uniformity to the effects of an environmental change than would those belonging to a composite stock, consisting of a number of lines. It is quite conceivable that among these last some would respond in a much greater measure than others. Or indeed some might not be affected at all. But here the much-scorned "mass statistics" would reveal the mean tendencies of the two lots, and the resulting data, though confessedly capable of further analysis, would be none the less valuable. If it be objected that the differences between the two averages may be due to the presence in one or both of the contrasted lots of a few "mutants," while the remaining individuals may not have been affected at all, I will only point out, as above, that the frequency distributions are directly opposed to such an assumption.

Having produced modifications of the sort mentioned, it remained to be seen whether these effects persisted beyond the generation immediately influenced. . . . (This part of the discussion, including an account of the method employed, the results, and certain of the possibilities of interpretation, I have thought it best to omit here, in view of the fact that I have covered practically the same ground in statements already published. I will merely note that the offspring of warm-room and cold-room mice, although themselves reared under identical temperature conditions, presented differences of the same sort as had been brought about in their parents through the direct effect of temperature, viz., differences in the mean length of tail, foot and ear.)

There remain two principal alternative explanations, which are not wholly distinguishable from one another, and neither of which admits of being stated except in rather vague terms.

One of these is the assumption that the changes undergone by the parent body are in some way registered in the germ cells, so as to be repeated, in a certain measure, in the body of the offspring. This conception has taken various forms, commencing with Darwin's hypothesis of "pangenesis." The same general view has recently been restated in chemical terms, and in a manner which is perhaps far less shocking to our common sense.

The other alternative is that of a "parallel induction" or "simultaneous modification of the germ-plasm," through the direct action of the modifying agent. This explanation, as we all know, has been freely used by Weismann and others to account for a considerable range of phenomena, notably the persistence of temperature effects in a second generation of butterflies. The phrase has indeed become so familiar through long repetition that few of us stop to consider just what it implies. "Parallel modification of the germ-plasm?" How can the unformed material of the germ cells be modified in the same manner as certain groups of somatic cells—say in a butterfly's wing—even by an all-pervading influence like temperature? This is obviously not what is intended. What we mean, concretely stated, is this: the germinal matter is so affected by the temperature that, after some hundreds or thousands of cell generations, certain of the resulting cells will show peculiarities in their pigment-producing powers of the same nature as those which arose directly in the somatic cells of the parent. And a most curious feature of this coincidence is that these modified cells are situated in precisely the same parts of the body in the one case as in the other.[7]

Thus do these very simple explanations have a way of losing their simplicity when examined critically. In the present instance, the hypothesis stated may, for all we know, be the one that most nearly represents the truth. But it should be stated frankly, in all its complexity, and not palmed off upon us as a readily intelligible hypothesis, which relieves us of the necessity of adopting an "inconceivable" one such as that of pangenesis.

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[7] Weismann's "determinant" hypothesis offers at least a *formal* solution of this difficulty, but I think that most biologists will agree with me that the solution thus offered is almost wholly a formal one.

In the case of a warm-blooded animal, of course, such an explanation as the foregoing could not be offered without still further modification. It might be conceded that temperature, as such, could not affect the germ-cells to any appreciable extent. But it might, on the other hand, be contended that the effects of temperature, even upon the parent body itself, may not be direct, but may be due to the formation of specific chemical substances, which, through the medium of the blood, may be supposed to simultaneously influence the body and the germ-cells. Thus we should, after all, be invoking a ''simultaneous modification of the germ-plasm,'' as in the case of cold-blooded animals.

Such a conception, vague as it is, has certain decided elements of strength. Let me point out, however, as I have already done more than once, that any such chemico-physiological mechanism as is here assumed would be of nearly or quite the same value for evolution as the ''inheritance of acquired characters'' in the old sense. An interpretation of this sort might ''save the face'' of certain speculative students of heredity, but the difference between the two views would have little but academic interest.

At the present time, I am continuing these experiments with mice, and am not only using much larger numbers than hitherto, but am resorting to several variations of the original theme, by which I hope to reduce the number of possible interpretations to a minimum. A friend wrote to me recently, wishing me no end of ''good results, *not Lamarckian.*'' This doubtless represents the attitude of a large number of persons toward the whole subject. By many, anything with a taint of ''Lamarckism'' about it would seem to be, *ipso facto,* beyond the pale of legitimate scientific investigation, belonging rather to the same category as pre-natal influences, telepathy and the ''borderland'' phenomena of psychical research. But the dawn of better times is already with us.

In conclusion, let me state that my own attitude toward this group of problems is one of indecision. If I confess to you, as I am bound to do, that positive results from my own experiments will give me far greater satisfaction than negative ones, this is chiefly because negative results commonly prove nothing. The question would be left very nearly as it was before. This, of course, constitutes a serious defect in my own vaunted method of attacking the problem, a defect which it shares, however, with any other which could be devised. But any results are better than no results, and these problems seem worth a far more thorough testing than they have yet received. The present experiments ought, as Professor MacDougal has pointed out,[8] and the author keenly realizes, to be subjected to various checks and controls, and to be continued through a considerable series of generations. It is my own fervent hope to be able to carry out such a program.

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[8] Presidential address before the American Society of Naturalists, read at Ithaca, December 29, 1910.